

Population dynamics of *Mortonagrion hirosei* (Odonata: Coenagrionidae)

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Abstract

The mark-and-recapture method was used to study the population dynamics of the endangered brackish water species, *Mortonagrion hirosei*, in a small reed community of an estuary in the warm-temperate zone of Japan. The flying season was from late May to early August. The age structure showed that newly emerged adults always stayed in the reed community and the maiden flight did not involve leaving the colony area. Although reed communities were abundant in the estuary, it appears possible that none or only very few of the individuals emigrated. Thus, both sexually immature and mature adults coexisted in the same reed community. The average distance covered by daily movements was 1.7 and 3.3 m for immature and mature males respectively, which were longer than those for females. Since the average durations of the immature and reproductive periods were respectively about 5 and 30 days in both sexes, the individuals may have moved less than 110 m throughout their life span, which corresponds to twice the length of the habitat. The estimated daily number of adults in the community was about 200 in 2000 and 500 in 2001. As the population was isolated, the estimated input of new individuals into the population had to be the number of individuals emerging. Thus, the total number of adults in both years was estimated to be about 5,000 and 6,000 respectively.

Introduction

Corbet (1999: 194) reviewed tolerance of high conductivity environments in Odonata. In Japan *Mortonagrion hirosei* Asahina is considered to prefer brackish water habitats and is classified as endangered on the IUCN red list, principally due to habitat loss. Adults have been found exclusively in reed communities. A number of brackish or saline water ponds and estuaries are distributed along the coast, and are characterized by reed communities. In recent years, however, practices such as river improvement and filling of wetlands have reduced the former ranges of reed communities. In Ise City, Mie

Prefecture, Japan, there are still many reed communities established in the brackish water of estuaries, but *M. hirosei* has been found at only a few sites, which are separated by several km from each other. The habitat consists mainly of slow-flowing streams with muddy bottoms. In general, the depth of water is less than 10 cm and most habitats are pure dense communities of the reed, *Phragmites communis*.

Throughout their life span, adult *M. hirosei* stay among the reeds, where they show reproductive behavior when sexually mature (Hirose & Kosuge 1973; Someya 1998; Fukui & Kato 1999). A number of odonate studies have revealed that the sexually immature period of adults is normally the principal period of odonate dispersal (e.g. Michiels & Dhondt 1991), and many odonate species fly a considerable distance away from water (Corbet 1999: 387). The immature adults of *M. hirosei*, however, do not leave their emergence sites, which is unusual (Watanabe et al. 1998). Parr (1973) showed that *Ischnura elegans* (Vander Linden) is a rare exception in that most immatures remain close to the water edge throughout the pre-reproductive period which in fact lasts several days. *M. hirosei* also appeared to need several days for maturation (Hirose & Kosuge 1973). Each *M. hirosei* population seems to be a relatively closed population, since its suitable habitats are isolated from each other (Someya 1998). The absence of detectable dispersal in immature *M. hirosei* makes the population structure of this species ideal for intensive study. However, little attention has been paid to the population ecology of *M. hirosei* in Japan, probably in part due to their cryptic coloring, which can cause them to be under-represented in a census (see Anholt 1997). Censusing is also difficult due to their small body size, weak flight activities, and the adoption of a sit-and-wait tactic when searching for prey or mates inside the reed community.

The aim of the present study was to obtain quantitative information on the adult population structure of *M. hirosei*. We used mark-recapture techniques to estimate the adult population size and the longevity and daily movements of individuals in an isolated reed community. We also observed the interactions among adults, which should help to clarify the *M. hirosei* mating system.

Study area and methods

A population of *Mortonagrion hirosei* was studied in an isolated reed community established on the estuary of Ise City. The habitat consisted of a small, relatively straight, slow-flowing stream (50 m long, 10 m wide), flowing into fresh water influenced by domestic waste and saline water at high tide. Human residents were on the north and paddy fields were on the south of the channel. Little pesticide was used on the paddy fields during the flying season. To the east the stream continued to Ise-Bay and the sea.

Adults of *M. hirosei* were recorded from late May to early August. The reeds were dense (440 live and withered stems per m²) and were used for oviposition and as the larval habitat. Adult censuses were carried out in the reed community on 31 and 32 mostly clear days in late May to early August of 2000 and 2001, respectively.

The habitat was subdivided into six sub-sites (about 100 m² each) to facilitate recording the location of individuals: two were in the northern and four in the southern part of the reed bed, including some areas outside the community. In 2000, the mark-recapture

method was carried out in only four sub-sites, mainly due to the soil condition of the reed community, which was too wet to access two sub-sites, and in 2001 all six sub-sites were used. It took about 3 h to patrol all sub-sites in the reed community. No reeds were trimmed in either study year; the community was about 2–2.5 m tall and the common height of the perching site of *M. hirosei* was usually less than 20 cm above the water.

Imagos were captured with a net in each sub-site and were anaesthetised by CO₂. Then, each *M. hirosei* was marked with its own number on the undersurface of the left hind wing using a black felt-tip pen. They were released at the same sub-site immediately after recording the date, sub-site number, sex and age. The marking was considered to have only minor effects on flight activities (and the probability of mating), since most of them began to fly normally and then to perch soon after recovering from the anaesthetic. Individuals injured during marking were treated as dead in the calculations. The age of each *M. hirosei* was estimated according to seven classes, mainly by wing condition and body colors, as in the case of other zygopteran species (e.g. Robertson 1985; Watanabe & Adachi 1987). The categories for males were as follows – T: newly emerged with soft gray bodies and soft wings; I: sexually immature with pale green thorax and gray eyes; II: older immature with green eyes; P: premature with light green thorax; M: mature with four bright green spots on the pronotum and a bright green ring on the eighth segment of the abdomen and wings with no visible damage; MM: older adult with yellow-green thorax and tattered wings; MMM: the oldest adults with discolored abdomen and very tattered brownish wings. For females, the same seven categories could be identified as follows. The body color and the wing condition of newly emerged females (T) were similar to those of males of the age T. Thereafter, the female body color became yellowish (I and II), but reddish-brown on the thorax (II). In addition, we identified females of age II, in which the first segment of the abdomen is red. The color of the female thorax then turned to moss-green when the female matured (the body color in age P is a transition phase). Females of age MMM could also be identified by a soiled abdominal tip due to oviposition. According to Corbet (1962), T, I, II and P are stages of the “pre-reproductive period” or “maturation period”, while the others (M, MM and MMM) are those of the “reproductive period”. Therefore, maturation of *M. hirosei* could easily be followed by coloration change and worn wing condition, although the coloration change in females was not as conspicuous as in males. In order to assess the individual size throughout the flying season, the length of the abdomen and hindwing were measured in young adults (age T and I).

Since the probabilities of recapture differed between the two sexes in most populations (e.g. Watanabe & Higashi 1989), the sexes of *M. hirosei* were processed separately through Jolly’s analysis (Jolly 1965).

Results

Mortonagrion hirosei has one generation per year. Unlike many zygopteran species, there was no distinct behavioral difference between males and females. Observations during the mark-and-recapture sampling (M. Watanabe & Y. Mimura unpubl.) showed that both sexes tended to stay mainly on dead reed stems with intermittent feeding flights, but did

not consistently defend perching sites against conspecifics. The spatial distribution of perching sites was roughly uniform. There was little difference in perching height among the adults; all perched about 20 cm above the water surface. Since females preferred darker sites in the reed bed than males, the probability of recapturing a marked female was somewhat lower than that of recapturing a marked male.

Adults were found throughout the whole habitat, but were sometimes concentrated on the margins of the community in early morning and late evening. These margins also supplied adult perching sites, although they were areas where potential predators, such as *Ischnura senegalensis* (Rambur), *Orthetrum albistylum speciosum* (Uhler), and birds, were active. We observed the capture of several *M. hirosei* by predators.

Figure 1 shows the changes in age distribution of captured adults in the study area throughout the flying season. In late May of both years, there were some sexually mature males but no mature females, suggesting that this species is protandric. Later, mature males became dominant, while mature females occupied a relatively small portion of the female population, partly due to low catchability, since they were cryptically colored and apt to stay among the dense stems inside the reed community. Individuals of age MMM were captured after late June in 2000 and early July in 2001. On the other hand, the emergence of *M. hirosei* in the habitat continued until late July, when the proportion of teneral females was about 1.5% of females present.

There were slight but statistically irrelevant changes in the body size of both sexes throughout the flying seasons of 2000 and 2001 (Fig. 2). The larger adults emerged first and the smaller adults emerged later, but the slight difference in body size did not correlate with any differences in behavior or longevity.

On the basis of the recapture data, the number of elapsed days in each age class was estimated (Table 1). For this calculation, only individuals appearing in each age class between the first and last captures were counted. Although both the duration of age II and P was significantly different between sexes, the sexually immature stage could last about 5 d. The duration of the stage MMM was not calculated according to the above definition, but we assumed that the duration was roughly equal to that of the other mature stages, M and MM, giving a total mature stage duration of about 30 d. Therefore, the maximum longevity was considered to be about 35 d, assuming none was captured by a predator.

After each distance between sub-sites had been measured, the daily shift of the capturing site for both sexes was calculated from the recapture data. Although the maximum distance moved between days for mature males was 31.7 m, immature males moved only about 1.7 m per day on average (Table 2). The distance moved increased significantly in mature males (3.3 m daily on average). Therefore, males moved about 8.5 m and 99 m during the immature and mature stages, respectively. Although there was no significant difference in the daily movement between immature males and females, females were more likely to stay at the same site throughout their lives.

Using Jolly's stochastic model (Jolly 1965), the daily change in the estimated number of males was similar to that of females, although the standard deviation for the females was larger (Fig. 3). The weather was unfavorable between survey days from late June to early July of 2000, resulting in few *M. hirosei* captures, and due to the low number of sub-sites surveyed, the estimated daily population for the year 2000 was lower than that of 2001. On the other hand, a single peak can be detected for each sex: about 500

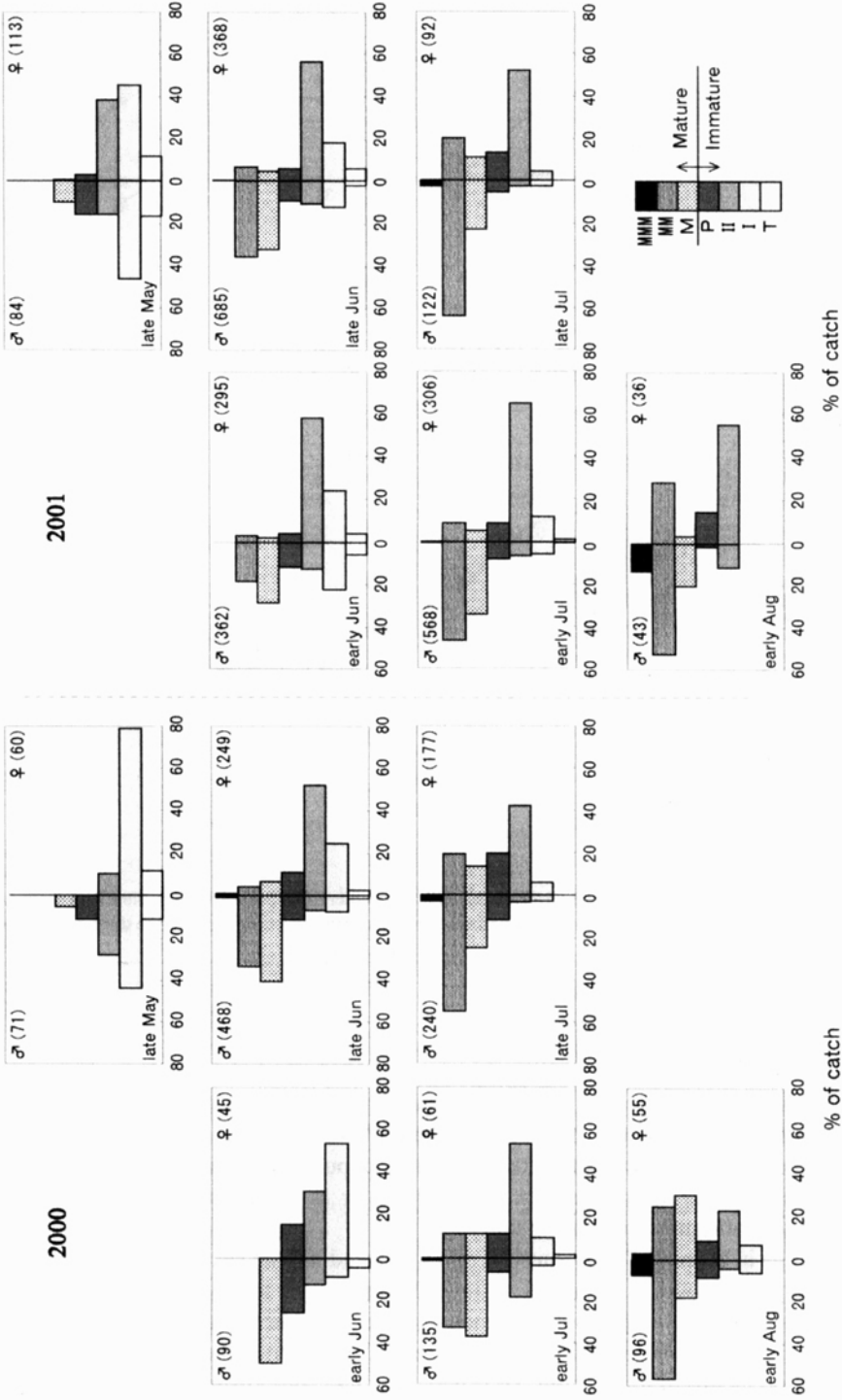


Figure 1. Age distribution of both sexes of *Mortonagrion hirosei* during the flying seasons of 2000 and 2001. T, I, II and P represent the sexually immature stages and M, MM and MMM the sexually mature stages. Numbers indicate the number of adults captured during the half-month measurement period.

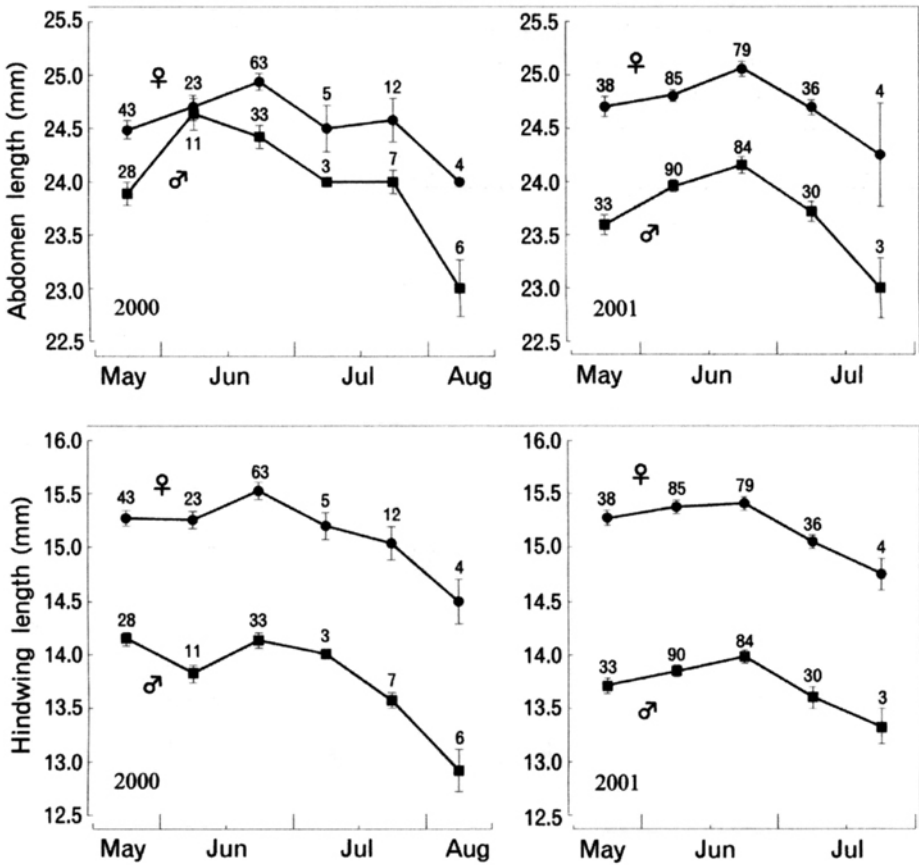


Figure 2. Changes in the size of immature *Mortonagrion hirosei* emerging (T and I) during the flying seasons of 2000 and 2001. Each bar represents s.d. The numbers above the symbols show sample size during the half-month measurement period.

males in early July and 1,000 females in late June of 2001. Each daily estimated number of females was larger than that of males, but each variance was also larger than that of males, probably due to the low recapture rate. Assuming that the sex ratio in this reed community was 1:1, we calculated the whole population by doubling the number of males, and the population density was then 2 per m^2 . We also assumed that the operational sex ratio must be close to unity.

The change in estimated daily survival rate fluctuated in both sexes between 0.46 and 0.82 in 2000, and between 0.69 and 1.42 in 2001 throughout the flying season (Fig. 4). Assuming a constant rate of survival in each age class, the mean daily survival rates in males were 0.64 and 0.80 in 2000 and 2001, respectively. Thus the mean longevity of males (L) was calculated to be about 3 d (2000) and 5 d (2001) using the equation

Table 1. Duration of each age class of *Mortonagrion hirosei*, based on the recapture data (days, \pm s.e.), using Mann-Whitney *U*-test. T, I, II and P represent the immature stages and M, MM and MMM the mature stages.

Year	Age class	♂	<i>n</i>	♀	<i>n</i>	<i>U</i>	<i>p</i>
2000	T	1.0 \pm 0.00	2	1.0 \pm 0.00	6	—	—
	I	—	—	1.0	1	—	—
	II	—	—	—	—	—	—
	P	1.3 \pm 0.14	12	1.9 \pm 0.10	10	26.0	$p < 0.01$
	M	7.0 \pm 1.10	5	5.0	1	—	—
	MM	9.7 \pm 2.60	3	—	—	—	—
	MMM	11.0	1	—	—	—	—
2001	T	0.9 \pm 0.04	25	0.9 \pm 0.04	26	315.0	n.s.
	I	1.1 \pm 0.16	8	1.2 \pm 0.09	26	109.0	n.s.
	II	1.7 \pm 0.31	7	2.6 \pm 0.10	76	407.5	$0.01 < p < 0.05$
	P	0.9 \pm 0.11	16	1.7 \pm 0.18	7	98.5	$p < 0.01$
	M	9.3 \pm 1.49	6	—	—	—	—
	MM	11.0 \pm 1.04	13	—	—	—	—
	MMM	—	—	—	—	—	—

Table 2. Length of daily movement [m \pm s.e.] of *Mortonagrion hirosei*, based on the recapture data among sub-sites in 2001.

Age class	Length of daily movement			
	♂	<i>n</i>	♀	<i>n</i>
Within immature stage	1.7 \pm 0.9 ^a	101	0.7 \pm 0.3	283
From immature to mature stage	1.3 \pm 0.4	124	1.4 \pm 0.9	12
Within mature stage	3.3 \pm 0.7 ^{a,b}	266	0.0 \pm 0.0 ^b	13

^a $U = 14,875.5$; $p < 0.01$

^b $U = 2,021.5$; $p < 0.01$

$$L = 1/(1-S)$$

where *S* is the daily survival rate.

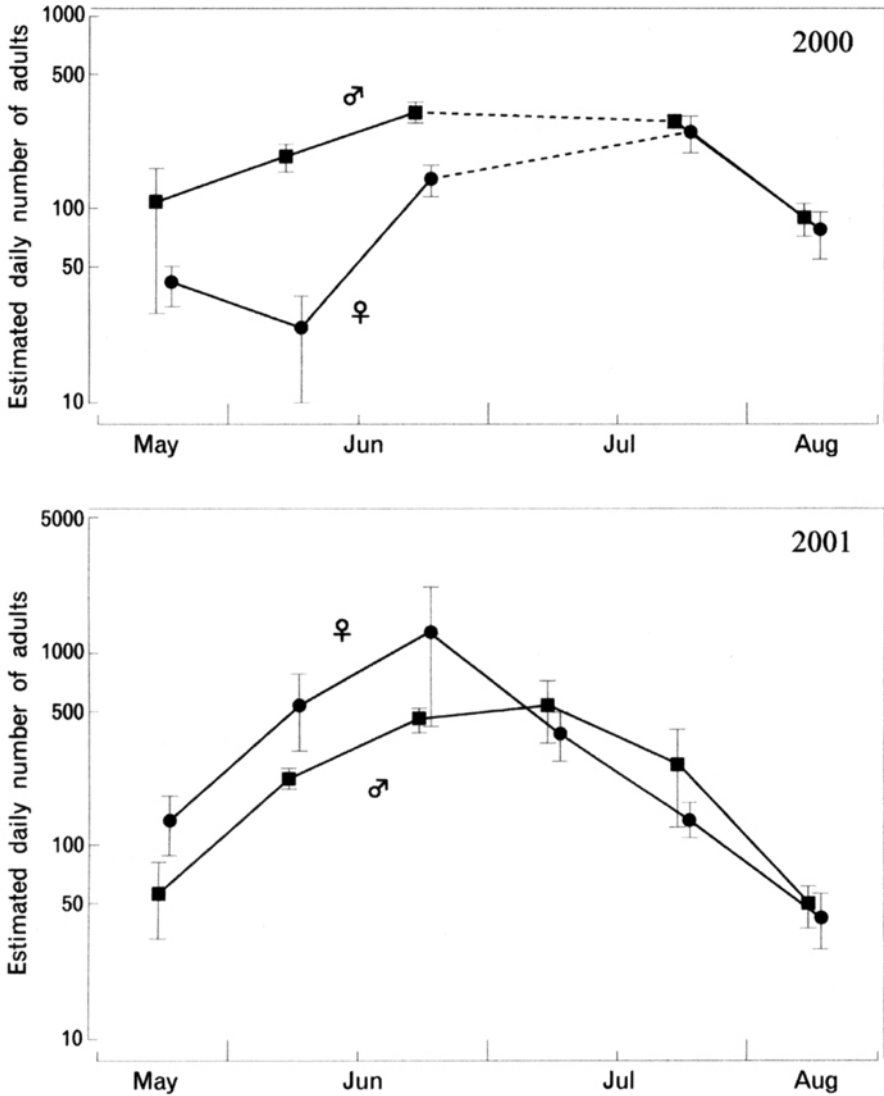


Figure 3. Changes in the estimated daily numbers of *Mortonagrion hirosei* in the reed community (50 m \times 10 m) in the half-month measurement periods during the flying seasons of 2000 and 2001. Each mean daily number was based on 5 sampling days. Each bar represents s.d.

Changes in the estimated number of new individuals recruited into the population over one and a half month intervals are shown in Figure 5. Because the habitat was isolated, the immigration and emigration rates of imagos in the *M. hirosei* population should be very low throughout the flying season. Therefore, the number of 'immigrants' into the population was taken as the number of teneral adults that emerged in the habitat.

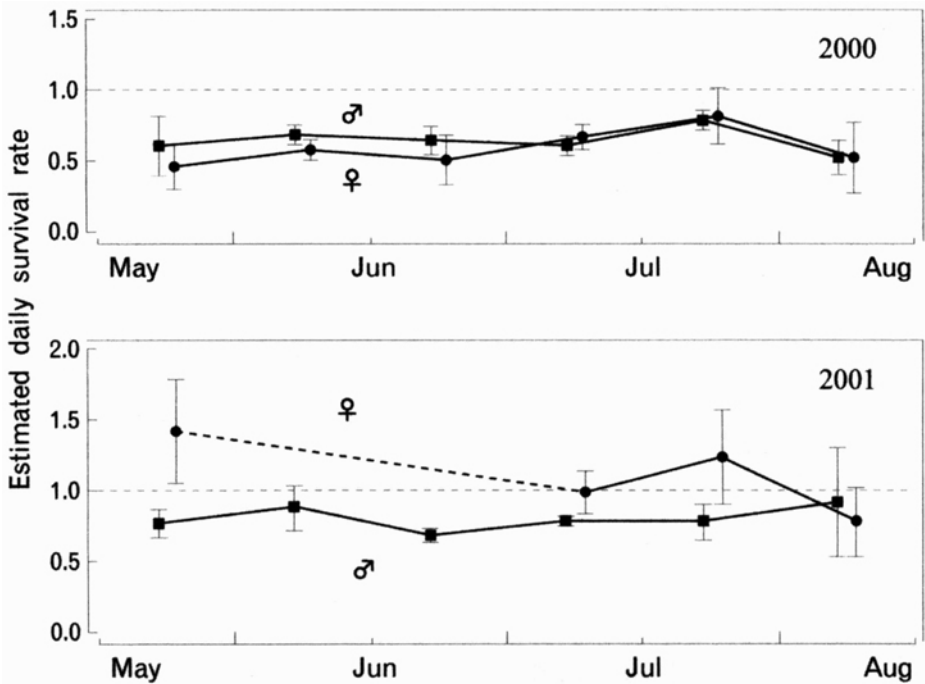


Figure 4. Changes in the estimated daily survival rate of *Mortonagrion hirosei* in the reed community in the half-month measurement periods during the flying seasons of 2000 and 2001. Each bar represents s.d.

Figure 5 shows the emergence curve for both sexes. The peak of emergence of males was earlier than that of females, also suggesting protandry. Since the estimated number of emerging females was likely to be overestimated, we simply doubled the number of males to arrive at a whole population number in the habitat per year, resulting in population numbers of about 5,000 and 6,000, for 2000 and 2001, respectively.

Discussion

Our study revealed that *Mortonagrion hirosei* is restricted to a small habitat where it shows little flight activity and maintains a stable population. The methods available do not allow us to trace rare events such as the possible migration of a small percentage of the population. Some of our results coincide with fragmental information made by Hirose (1985), that this species always stays down amongst the reeds in communities established in brackish water. However, we did not observe territorial behavior, as described by Hirose & Kosuge (1973). The high density in the reed community throughout the flying season suggests that this species does not exhibit territoriality, though a certain level of intraspecific aggression, such as face-to-face hovering between sexes and between immature and mature adults, was observed (M. Watanabe & Y. Mimura unpubl.).

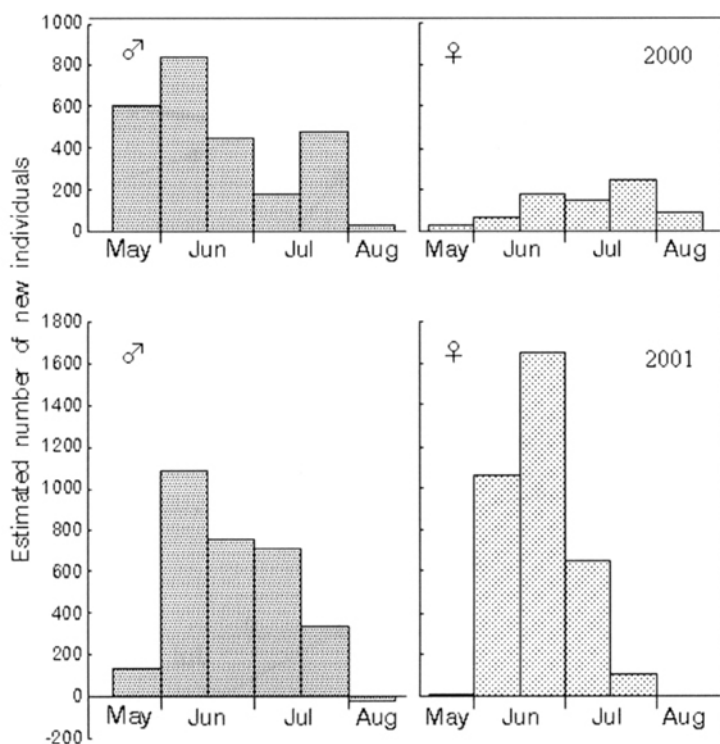


Figure 5. Changes in the estimated number of new individuals recruited into the population of *Mortonagrion hirosei* in the reed community in the half-month measurement periods during the flying seasons of 2000 and 2001.

Weather conditions at the study site changed dramatically during the flying season of *M. hirosei*. The weather was fine for both the onset of emergence and the late flying season, while the middle of the flying season coincided with the monsoon rainy season of Mie Prefecture. Anholt et al. (2001) pointed out that zygopteran species seem to survive very well in protected places on rainy days. Rain can reduce the survival of Zygoptera, but it may need to be very heavy or persistent to do so (Cordoba-Aguilar 1993; Heymer 1973). However, in the microhabitat of *M. hirosei*, strong winds and heavy rain did not inhibit their normal behavior, such as perching postures, cruising flight or reproductive behavior. The available space for *M. hirosei* activity in the reed habitat must be comparable to that of the dense forest floor (M. Watanabe & Y. Mimura unpubl.). Consequently, the inclement weather might not have affected the population, but simply decreased the number of favorable sampling times.

M. hirosei is phylogenetically close to *M. selenion* Ris, which is well known to inhabit paddy fields and other open wetlands (Hirose & Kosuge 1973; Mizuta 1974). The two species co-exist in our survey area, though *M. selenion* is multivoltine, and

flies above the paddy fields as a part of its reproductive behavior, and along the margins of the reed community in cruising flights. *M. selenion* prefers open land, and actively behaves as a flyer (Corbet 1962), unlike *M. hirosei*. Therefore, no odonate species coexists with *M. hirosei* in the reed community. A census of larvae in April 2000 also showed no odonate larvae except *M. hirosei* inhabiting the reed community in brackish water (M. Watanabe & Y. Mimura unpubl.).

Although *M. hirosei* normally spends much time amongst the reeds and uses a sit-and-wait foraging tactic in order to catch prey, its small body size and weak flight habits may lead to an increased risk of predation, particularly at the water's edge (e.g. Banks & Thompson 1987; Anholt 1992). Males may suffer higher mortality associated with their brighter coloration compared to females. As the females oviposit alone, any risk associated with this would be borne alone. Anholt (1997) showed that immature females of *Lestes disjunctus* Selys have lower survival rate to sexual maturity than males. A prolonged maturation period in females might also reduce survival to sexual maturity, as suggested by Fincke (1987). Therefore, in addition to sexual differences in behaviour, the mortality cost may also lead to a biased sex ratio, usually an operational male-biased sex ratio (Corbet 1999: 301). The maiden flight plays a role in dispersal for both sexes of many odonate species, resulting in apparently low survival at the water where they emerge (Utzeri et al. 1988; Corbet 1999: 299). There seems to be little difference in the duration of the immature stage of *M. hirosei* between sexes, and they have no maiden flight of long distance.

Although the females of *M. hirosei* were harder to catch because of their cryptic coloration and less conspicuous behavior, the sex ratios based on the estimated daily numbers throughout the flying season of two years appeared to be roughly 1:1. This is not always the case with Zygoptera, particularly in species adopting territorial tactics, where mature males return to the water to establish territories but mature females tend to visit only to mate and oviposit. Then, the probability of recapture for territorial males is higher than that for females (Watanabe & Taguchi 1988). However, females of *M. hirosei* stay in the reed community together with males, without a maiden flight of any great distance away from the emergence site, as in the case of *Calopteryx japonica* Selys (Watanabe et al. 1998), in which little movement of females away from their emergence site is reflected in the observed stable population parameters. We did not detect any difference in daily survival between sexes, but the estimates of mean life span calculated from these survival rates in both sexes (ca 3–5 d) are within the range previously reported for Zygoptera (e.g. Thompson 1989; Bennett & Mill 1995; Corbet 1999: 300). Miyakawa (1982) reported that the mean longevity of *C. japonica* in Saitama Pref. was the same between sexes that coexisted in the same area. However, the life span of *M. hirosei*, estimated from the calculation of Jolly's model, may be seriously underestimated in spite of their restricted distribution in the reed community. Corbet (1999: 302) concluded that the median of maximum adult longevity in 23 zygopteran species was 29.8 days; this is comparable with our estimates of about 35 days for *M. hirosei* based on the duration of each age class using mark and recapture data.

The daily population density of *M. hirosei* was high (2 adults per m²) and the distribution appears to be roughly regular. The abundance of reed stems (440 stems per m²) also appeared to support the regular distribution of the potential perching sites, where the

average distance between stems was about 5 cm (M. Watanabe & Y. Mimura unpubl.). Watanabe & Matsunami (1990) showed that the distribution of male *Lestes sponsa* (Hansemann) was random on the forest floor because they established territories at the sunflecks randomly distributed in the forest. Cordoba-Aguilar (1994) pointed out that more aggressive males of *Hetaerina cruentata* (Rambur) were more abundant in substrates closer to the water. The distribution of the female *H. macropus* Selys reflects where they feed rather than where they breed (Eberhard 1986).

The coexistence of mature and immature individuals as well as of both sexes in the restricted area can be expected to affect flying and reproductive behavior. Females of *M. hirosei* tended to move only short distances between perching sites, while mature males flew much farther between perching sites. Although the mature males moved about 3.3 m daily, the difference in flight activity suggests that the reproductive process must occur within the reed community. For the purpose of population genetics, the population is a single unit, even with low dispersal movement.

Most odonate females are polygamous, although it has frequently been reported that they can refuse to copulate (Corbet 1999: 471). In the case of *M. hirosei* staying in the reed community, the high density seems to discourage mature males from attacking or harassing immature or mature single females for the purpose of mating. In fact, in our study, the adults were exclusively found perching low, near the water surface on the stems of dense reeds, on dark perching sites probably with very poor visibility. There must be an additional mechanism to prevent releasing unnecessary courtship behavior. This is probably their lifetime habit as a percher. Although further detailed behavioral study of this species is needed, our results make clear the importance of the dense reed community for the life history of *M. hirosei* in brackish water estuaries. It is apparent that dragonflies are good indicators of habitat types and the ecological quality of the land-water-interface because of their complex habitat requirements (see review in Corbet 1999: 9f). In the species studied, the effect of habitat fragmentation (loss of suitable reed communities) is likely to lead to isolation effects. A study by Kiauta & Kiauta (1988) on *Coenagrion mercuriale* (Charpentier) demonstrated that such isolation effects can lead to measurable genomic changes which may increase the sensitivity of the species to adverse environmental factors and thus increased risk of extinction. This aspect further increases the indicator potential of the species in the estuarine ecosystem and has a positive effect on the evaluation of conservation strategies.

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References

- Anholt, B.R., 1992. Sex and habitat differences in feeding by an adult damselfly. *Oikos* 65: 428-432.
- Anholt, B.R., 1997. Sexual size dimorphism and sex-specific survival in adults of the damselfly *Lestes disjunctus*. *Ecological Entomology* 22: 127-132.
- Anholt, B.R., C. Vorburger & P. Knaus, 2001. Mark-recapture estimates of daily survival rates of two damselflies (*Coenagrion puella* and *Ischnura elegans*). *Canadian Journal of Zoology* 79: 895-899.
- Banks, M.J. & D.J. Thompson, 1987. Lifetime reproductive success of females of the damselfly *Coenagrion puella*. *Journal of Animal Ecology* 56: 815-832.
- Bennett, S. & P.J. Mill, 1995. Pre- and post-maturation survival in adults of the damselfly *Pyrhosoma nymphula* (Zygoptera: Coenagrionidae). *Journal of Zoology* 235: 559-575.
- Corbet, P.S., 1962. A biology of dragonflies. Witherby, London.
- Corbet, P.S., 1999. Dragonflies: behavior and ecology of Odonata. Cornell University Press, New York.
- Cordoba-Aguilar, A., 1993. Population structure in *Ischnura denticollis* (Burmeister) (Zygoptera: Coenagrionidae). *Odonatologica* 22: 455-464.
- Cordoba-Aguilar, A., 1994. Male substrate use in relation to age and size in *Hetaerina cruentata* (Rambur) (Zygoptera: Calopterygidae). *Odonatologica* 23: 399-403.
- Eberhard, W.G., 1986. Behavioral ecology of the tropical damselfly *Hetaerina macropus* Selys (Zygoptera: Calopterygidae). *Odonatologica* 15: 51-60.
- Fincke, O.M., 1987. Female monogamy in the damselfly *Ischnura verticalis* Say (Zygoptera: Coenagrionidae). *Odonatologica* 16: 129-143.
- Fukui, J. & T. Kato, 1999. [Life history of *Mortonagrion hirosei* in the estuary of Toda River. In Japanese]. *Suruga-no-Kontyu* no. 185: 5170-5178.
- Heymer, A., 1973. Verhaltensstudien an Prachtlibellen. Fortschritte der Verhaltensforschung, Beihefte zur Zeitschrift für Tierpsychologie 11: 1-100.
- Hirose, M., 1985. The present state of *Mortonagrion hirosei*, a new species of dragonfly first discovered in 1971. *Collecting and Breeding* 47: 390-391. [In Japanese].
- Hirose, M. & T. Kosuge, 1973. [Life history of *Mortonagrion hirosei* in Hinuma pond, Ibaraki Prefecture. In Japanese]. *The Nature and Insects* 8(4): 2-6.
- Jolly, G.M., 1965. Explicit estimates from capture-recapture data with death and immigration-stochastic model. *Biometrika* 52: 225-247.
- Kiauta, B. & M. Kiauta, 1988. The unusual recombination potential and its ecological implications in *Coenagrion m. mercuriale* (Charp.) from Liechtenstein (Zygoptera: Coenagrionidae). *Notulae Odonatologicae* 3: 34-35.
- Miyakawa, K., 1982. Reproductive behavior and life span of adult *Calopteryx atrata* Selys and *C. virgo japonica* Selys (Odonata: Zygoptera). *Advances in Odonatology* 1: 193-203.
- Mizuta, K. 1974. Ecological and behavioral isolation among *Mortonagrion selenion* Ris, *Ceriagrion melanurum* Selys, and *Copera annulata* (Selys) (Zygoptera: Coenagrionidae, Platynemididae). *Odonatologica* 3: 231-239.
- Parr, M.J., 1973. Ecological studies of *Ischnura elegans* (Vander Linden) (Zygoptera: Coenagrionidae). I. Age groups, emergence patterns and numbers. *Odonatologica* 2: 139-157.
- Robertson, H.M., 1985. Female dimorphism and mating behaviour in a damselfly, *Ischnura ramburi*: females mimicking males. *Animal Behaviour* 33: 805-809.
- Someya, T., 1998. The present state of the damselfly, *Mortonagrion hirosei*. *The Nature and Insects* 33(10): 4-8. [In Japanese; English title].

- Thompson, D.J., 1989. A population study of the azure damselfly *Coenagrion puella* (L.) in northern England. *Journal of the British Dragonfly Society* 5: 17-22.
- Utzeri, C., G. Carchini & E. Falchetti, 1988. Aspects of demography in *Lestes barbarus* (Fabr.) and *L. virens vestalis* Ramb. (Zygoptera: Lestidae). *Odonatologica* 17: 107-114.
- Watanabe, M. & Y. Adachi, 1987. Fecundity and oviposition pattern in the damselfly *Copera annulata* (Selys) (Zygoptera: Platycnemididae). *Odonatologica* 16: 85-92.
- Watanabe, M. & M. Taguchi, 1988. Community structure of coexisting *Sympetrum* species in the central Japanese paddy fields in autumn (Anisoptera: Libellulidae). *Odonatologica* 17: 249-262.
- Watanabe, M. & T. Higashi, 1989. Sexual difference of lifetime movement in adults of the Japanese skimmer, *Orthetrum japonicum* (Odonata: Libellulidae), in a forest-paddy field complex. *Ecological Research* 4: 85-97.
- Watanabe, M. & E. Matsunami, 1990. A lek-like system in *Lestes sponsa* (Hansemann), with special reference to the diurnal changes in flight activity and mate-finding tactics (Zygoptera: Lestidae). *Odonatologica* 19: 47-59.
- Watanabe, M., M. Taguchi & N. Ohsawa, 1998. Population structure of the damselfly *Calopteryx japonica* Selys in an isolated small habitat in a cool temperate zone of Japan (Zygoptera: Calopterygidae). *Odonatologica* 27: 213-224.